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Functional analysis of the surfacing behaviour in the harbour porpoise, *Phocoena phocoena* (L.)

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Introduction

The most well-known behaviour of porpoises is their smooth, rolling way of surfacing when they breath. Observations made by Spencer et. al. (1966) on the Killer whale, *Orcinus orca,* indicates that the respiratory act includes "orienting movements of a dorsal flexure of the thorax, and integrated flipper, fluke and body movements brought together in a complex involuntary act preceding the movement of air".

Such movements are seen in beached animals (Spencer et al. 1966), in surface sleeping ones (McGormick 1969), and according to the latter author, the absence of the tail movements are used to indicate depth of anesthesia, being the last movements to disappear before surgical plane is reached.

Spencer et. al. (1966) also investigated the duration of a blow (expiration and inhalation) and the action of the blowhole in the Killer whale. They found a mean expiratory duration of 0.38 seconds, and a mean inspiratory duration of 0.78 seconds. The expiration was performed through a pursed blowhole, while it was fully open during the inhalation.

This study was conducted to give a more detailed description of the movements referred to above.

Most studies of dolphin behaviour – and quite an impressive bulk of knowledge has been gathered – have been of a descriptive character, and the endpoint of such studies is a so called ethogram. This ethogram must not be considered as a final end, but only as a base for analytic work bringing about an understanding of the behaviour of these animals. Unfortunately, very little analytic work has been done up to date, possibly in part due to the very special, and rather ununiform "dolphin terminology", quite remote from that used on other animals.

Therefore it would be very desirable for a future comparative analysis if students of dolphin behaviour would adopt the ethological methods and terminology.

Materials and methods

The study is based on 8-mm movie pictures, drawn step by step. The time indications in the figures are given in seconds, and are calculated from the number of frames. The film speed was 18 frames per second. As the figures are prepared from different film sequences, there is some variation in the duration of the phases in the behaviour.

The animals were kept in a 40 m² pool with a water depth of 1 m. They were at the occasion around one year old and was captured about one month prior to filming.

Z. Säugetierkunde 39 (1974) 313—318

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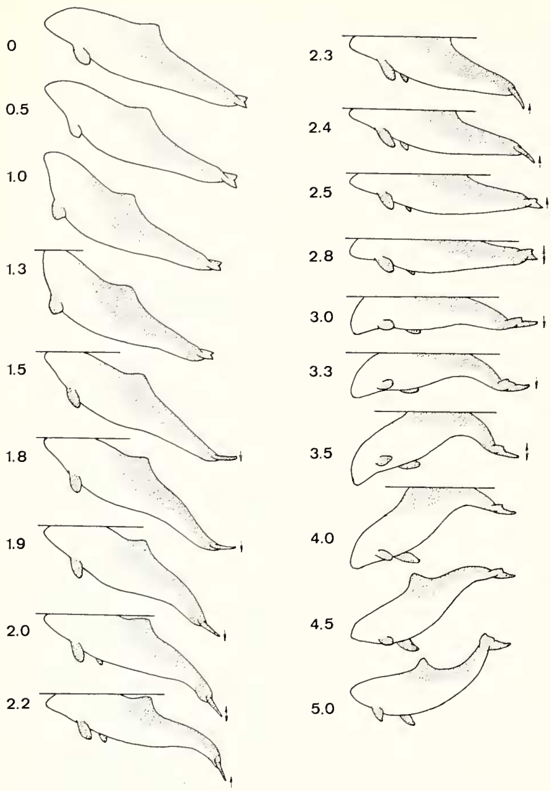


Fig. 1. A normal porpoise surfacing roll. (Explanations to the figures are given in the text. The time base is given in seconds.)

Results

Body movements during a normal roll

Several interesting features can be seen in fig. 1, where the normal porpoise roll is followed step by step. It is seen that the initial part consists of a pronounced bending up of the thorax (0.5–1.3 seconds). When the surface is reached, the tail is struck down, and the head resumes its normal position, why the thorax levels out (1.5–2.0 seconds). Then follows a powerful upward tail-stroke, where after the animal lies parallel to the surface (2.2–2.8 seconds). To support the ensuing bending down of the thorax, the tail is arched downwards, wich raises the tailstock above the water. This constitutes the last part of the roll, and after the short downstroke, the tail is held passive until it is well under the surface.

Blowhole operation

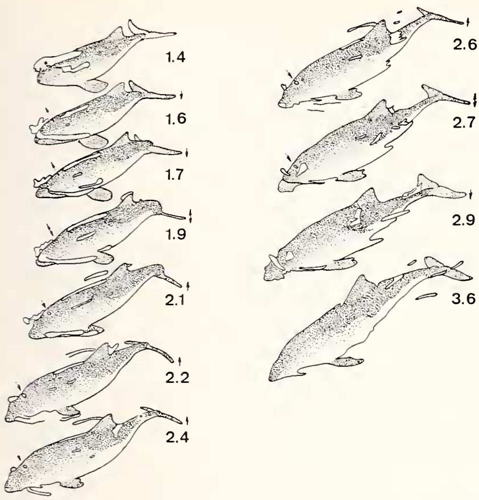
Fig. 2 shows the synchronization of the tail beats and the opening of the blowhole. Between 1.6 and 1.7 seconds, during the downstroke with the tailfin (cf 1.5–2.0 seconds in fig. 1), the lungs are emptied. The succeeding upstroke with the tail is accompanied with the inhalation (2.1–2.7 seconds, cf 2.2–2.8 seconds in fig. 1), and the closure of the blowhole is effected when this tail beat is finished (around 2.7 seconds). Then the head is bent down, and the blowhole becomes submerged.

As seen in fig. 3, the expiration is performed with the blowhole only partly open. During the inhalation the blowhole is wide open and also somewhat "sucked inward".

Pectoral fin movements

Indicated in fig. 1, although not especially clear, are the movements of the pectorals. These movements are very minute, why a closer film sequence had to be taken. This sequence is shown in fig. 4.

The upward flexure of the head (0.9–1,4 seconds, cf 0.3–1.3 seconds in fig. 1), is, partly, effected with a steering of the pectoral fins, i. e. the tip of the fin is moved downward and the trailing edges are turned forward, towards each other, thus putting an upward pressure upon the body.



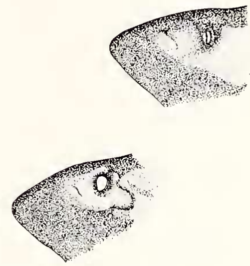


Fig. 3. Close view of the blowhole, showing the difference between the expiratory (above) and inhalatory phase

Fig. 2. Sequence showing the synchronization of the tail-beats and breathing. The pictures are distorted because the original film was taken from above, partly through the water surface. The arrow at the blowhole show direction of air-flow

During the downstroke with the tailfin (cf 1.5—2.0 seconds in fig. 1), the tip and trailing edge of the pectoral fin are turned upward (1.4–2.0 seconds), and the resulting downward pressure assists the leveling out of the body. During the upstroke (2.2–2.9 seconds, cf 2.2—2.8 seconds in fig. 1), the pectorals are adjusted in approximately the same way as during the initial part, i. e. they steer upwards, lifting the head above the water when the animal inhales (cf 2.1—2.7 seconds in fig. 2).

In order to find out how important a role the pectorals played, an approximately half-year-old animal was let loose in the pool with his fins tied tightly against the body. However, this did not make much difference, but the animal was able to surface quite normally.

Discussion

Functional analysis

The results presented here reveale a beautifully coordinated sequence of movements, typical of the gracious dolphin behaviour.

The synchronization of blowhole opening and tail movements are no coincidence, but ensures that the blowhole is above the water at the breathing. Besides that, it is rather natural that the expiration is accompanied with a downward flexure, because of the contraction of the diaphragm and the abdominal muscles. Likewise the inhalation, i. e. the muscular expansion of the lungs, causes an upward flexure of the body.

The downward tail stroke has two functions; firstly it initiates the leveling out of the body, secondly, it put the tailfin in a position that makes the succeeding upstroke possible. Bearing in mind that the thrust is provided by the upstroke (Purves 1968; van Heel 1968), the angle of the tailfin during the downstroke can be understood as being an upward steering with the tail.

The upstroke hat several functions. It completes the leveling out (with the aid of the pectorals), it provides thrust, ensuring "steering speed" to the pectoral fins, and creating a bow wave in front of the melon — vital at least in calm weather — that

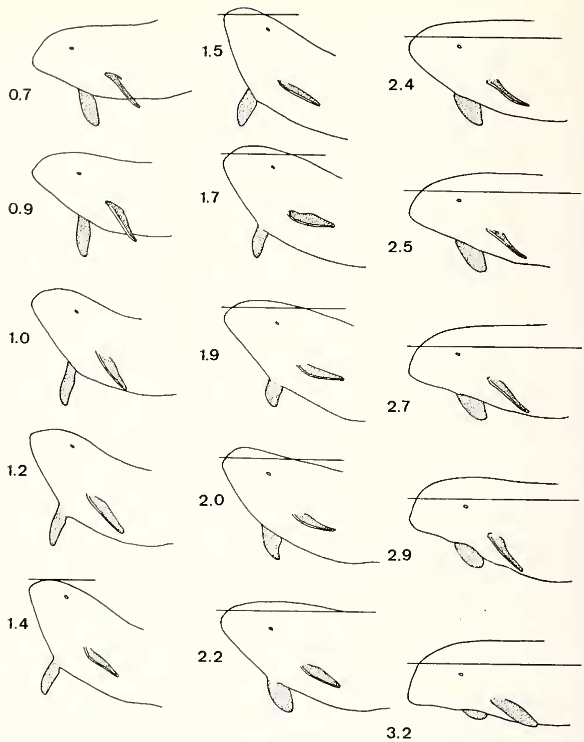


Fig. 4. The movements of the pectoral fins during the first part of the surfacing roll

keeps the blowhole dry during the inhalation. The speed also facilitates submerging, although it is the tailstock, raised above the water, that actually presses down the body. In many whale species, as well as in human divers, this downward pressure is increased by raising the hole tail and legs respectively above the water.

Breathing time

In fig. 2 can be seen that the blow lasts for about 1.1 seconds. Judged from the tail movements in fig. 1 and 2, the expiration and inhalation can be separated, and average 0.4 and 0.8 seconds respectively. Surprisingly enough this is very close to the measures from the much larger killer whale, *Orcinus orca,* mentioned in the introduction. It should be pointed out, though, that the harbour porpoise measures are confined to rather low level activities. In other situations, e. g. in fright reactions, the whole breathing sequence appears much shorter, and then the amplitude of the tail beats are also smaller.

Chest and throat movements

The peculiar form of the chest and the throat, just at the end of the inhalation (2.9 seconds in fig. 3), is no artifact. At present, however, the exact cause of these are not known, but possibly the "bulb" in the throat region is connected with the larynx action, e. g. when the epiglottal orifice is closed. The bulb in the chest region may be caused by the sternum, that due to the absence of clavicles, has no fixed position, but is rather free to move during the breathing.